

6.—ACTINOSIPHONATE CEPHALOPODS (CYRTO-
CEROIDA) FROM THE DEVONIAN OF
AUSTRALIA.

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ABSTRACT.

In Western Australia the group of nautiloids with actinosiphonate structure is represented by *Conostichoceras* and by *Wadeoceras*. On the basis of recent finds, the latter genus can be redefined. Also, the possibility of sexual dimorphism in this genus is discussed and its commensalism with crinoids described. In Victoria, the actinosiphonate group is represented by *Phragmoceras subtrigonum* McCoy which is here referred to the genus *Danaoceras* Foerste, as well as by a species of doubtful generic relationships, *Danaoceras ? bindiense*, both from the Middle Devonian of Gippsland.

ACTINOSIPHONATE CEPHALOPODS IN WESTERN AUSTRALIA.

In a recent paper I drew attention to the occurrence of actinosiphonate cephalopods (Cyrtozeroidea) in Western Australia where this group is represented by the probably Middle Devonian *Conostichoceras hardmanni* and the Upper Devonian *Wadeoceras australe*, both from strata in the Kimberley District in the northern part of the State (Teichert, 1939). The genus *Wadeoceras* was established in this paper on a rather fragmentary phragmocone. In July, 1939, I had the opportunity of visiting some of the Devonian localities in the Kimberley District and spent a day in the vicinity of Mt. Pierre. On this occasion I secured well preserved specimens of *Wadeoceras* so that the genus can now be fully described.

It was found that *Wadeoceras* occurs in the Middle Goniatite beds of the Kimberley District where it is associated with the goniatites *Cheiloceras*, *Tornoceras*, and *Dimeroceras*. The age of these beds corresponds to the Oberdevonstufe II or *Cheiloceras* stage of the European standard section as has been explained elsewhere (Teichert, 1940).

I wish to take this opportunity to express my gratitude to Mr. L. M. Waterford and to Dr. R. T. Prider who most readily rendered valuable assistance in the field, also to the Freney Oil Company, Ltd., Perth, who very kindly provided the facilities for my visit to the Kimberley District. The plates and text-figures in this paper were prepared by Mrs. Gertrude Teichert.

SEXUAL DIMORPHISM IN *WADEOCERAS*.

As will be more fully described below, *Wadeoceras* is represented in the new collection by two forms which resemble each other in many respects. One of the specimens (No. 19485) is so similar to the holotype of

Wadeoceras australe that the redefinition of the genus is largely based on this specimen. Another almost complete specimen (No. 19486) is very similar to typical *Wadeoceras australe* with which it agrees in the general shape and the proportions of the conch and in the position and structure of the siphuncle. It differs, however, in its larger size and in the greater length of its camerae. Both forms are represented by gerontic individuals, characterised by the shortness of the last camera and by the presence of the basal thickening of the wall of the living chamber ("basal zone" of Flower, 1938, p. 9). The larger specimen was found in a layer 12 feet above the layer which contained the smaller specimen. A fragment of another specimen of the smaller type (No. 19497) was found 63 feet above the large specimen (19486) and 40 feet below the lowest beds containing *Sporadoceras*. The larger specimen might represent a different species, but it seems more probable that we are here concerned with a case of sexual dimorphism.

Sexual dimorphism in fossil nautiloids was first discussed by Ruedemann (1919, 1921, 1926) when he studied a series of specimens of *Oncoceras* from the Ordovician Utica shale of New York. The specimens could be divided into three groups, two of which resembled each other very closely except for their size, and which Ruedemann, therefore, referred to one and the same species, *Oncoceras pupaeforme*. In view of the fact that in living cephalopods the males are usually more slender or smaller than the females, Ruedemann regarded the smaller specimens as the males and the larger specimens as the females of this species. In 1926 Foerste (p. 355) explained differences in the dorsal collar of specimens of *Inversoceras* as possibly indicating sexual differences.

The question of sexual dimorphism in cephalopods was again discussed by Flower in 1938 (pp. 7-8), who called attention to possible cases among species of *Ovoceras*, *Brevioceras*, and *Verticoceras* from the Devonian of New York. As a matter of fact, as Flower justly pointed out, "the existence of sexual dimorphism in extinct forms, and particularly in extinct forms which have no close living relatives, is not a thing that can be categorically asserted or denied," but the conditions in *Wadeoceras* agree well with cases which are thought to indicate existence of sexual dimorphism in other breviconic genera. In all the examples quoted by Flower the difference in size between the supposed females and males is not as pronounced as in Ruedemann's original example of *Oncoceras pupaeforme*. If our interpretation is to be accepted the sex distinctions in *Wadeoceras australe* are more marked than in the Devonian breviconic genera referred to by Flower and more similar to those of *Oncoceras pupaeforme*.

COMMENSALISM.

On both conchs of *Wadeoceras* described below there are erinoid roots attached to the shell, varying in size between one and six millimetres in diameter. These roots are irregularly scattered over the surface of the conch. It is therefore probable that they were attached to the conch while the animal was still alive, and it must be assumed that the animal either crawled along carrying its conch elevated in an inverted position, or, what is more likely, that it led an actively motile, nectonic life. As far as I am aware, cases of commensal erinoids adhering to nautiloid cephalopods have only been described once before, viz., by Ganss in 1937, who gave an excellent description of erinoid and cystoid roots attached to Ordovician orthoceroid and endoceroid conchs found in the Pleistocene drift of northern Germany.

Furthermore, the Department of Geology of the University of Western Australia possesses a specimen of a large *Pinacoceras* from the Upper Triassic of Bihati, Timor, invested by numerous crinoid roots on both sides of the conch. Similar cases among Triassic and Liassic ammonites were described by Ganss in a previous paper (1935). Miller, in 1932, observed that on the whole, commensal organisms are very rarely found on tetrabranchiate cephalopods and the occurrence of commensal crinoids on shells of Devonian *Wadeoceras* is, therefore, rather unusual and worth mentioning. It may be added that the beds containing *Wadeoceras* contain a fair amount of isolated crinoid stems and roots, though no parts of crowns have as yet been found.

ACTINOSIPHONATE CEPHALOPODS IN VICTORIA.

In my paper referred to above I suspected that *Phragmoceras subtrigonum* McCoy from the Middle Devonian of Victoria might be another representative of *Wadeoceras* in Australia. Thanks to the kindness of Messrs. D. J. Mahony and R. A. Keble, of the National Museum, Melbourne, I have since had the opportunity of studying the holotype and other specimens of this species. From these studies it was at once evident that the Victorian species belongs to a different genus, and it is here referred to the genus *Danaoceras* Foerste which has so far only been known from the Middle Silurian of Bohemia. *Danaoceras* is closely related to *Wadeoceras*, as pointed out by me in 1939, and both belong to the same family Archiacoceratidae. The geographical range of actinosiphonate cephalopods is thus extended right across the Australian continent from its north-western part to the south-east corner.

The group is also represented by one specimen from the Middle Devonian of Bindi which is a new species of somewhat doubtful generic affinities, and which is here described as *Danaoceras* (?) *bindiense* sp. nov.

In Victoria, *Danaoceras* is associated with several other species of nautiloids which, however, are in need of being restudied (1).

Danaoceras subtrigonum is characterised by a great number of endosiphuncular lamellae. These lamellae are lined with secondary deposits, apparently similar to those of *Jovellania* from the Devonian of France, as described by Dechaseaux in 1937.

PALAEONTOLOGICAL DESCRIPTIONS.

Genus **WADEOCERAS** Teichert.

Genotype—*Wadeoceras australe*, Teichert, 1939, p 111.

Emended diagnosis.—Endogastric poterioceroid cyrtoceracones with actinosiphonate siphuncle and constricted, phragmoceroid aperture with wide hyponomic sinus. Segments of siphuncle wider than long, but not inflated between the septa.

As has been pointed out before (Teichert, 1939) the genus is related to *Danaoceras* Foerste and to *Archiacoceras* Foerste. In the general shape of the conch it recalls *Poteriocerina* Foerste which, however, is an exogastric form.

(1) In 1939 (p. 106) I made reference to a few incorrect identifications of *Actinoceras* from Devonian rocks of the Australasian region. To these has to be added, in all probability, the recorded occurrence of *Actinoceras* in the Middle Devonian of Victoria and New South Wales (Benson, 1922, p. 114). I have examined one specimen, thus determined, from the Devonian of Cavan, Murrumbidgee River, Yass District, New South Wales (No. 7010, National Museum, Melbourne) which is an indeterminable fragment of a straight phragmocone.

Wadeoceras australe Teichert.

Plate I., Figs. 2, 3; Plate II., Figs. 4-6.

1939—*Wadeoceras australe*, C. Teichert, Jour. Roy. Soc. West. Austr., vol. 25, pp. 111-112, pl. 1, figs. 2, 3.

The holotype of this species is a portion of a phragmocone. There are now available two almost entire specimens which will be described here.

(1) No. 19485, Department of Geology, University of Western Australia, from strata 114 feet below the lowest bed containing *Sporadoceras*, on east side of crossing of the old road from Fitzroy Crossing to Hall's Creek over a small creek about half a mile west of the crossing of the same road over Mt. Pierre Creek. (Pl. I., fig. 3; Pl. II., fig. 4.)

This is an internal mould, 82 mm. long, consisting of portion of a phragmocone with 13 camerae and the living chamber which is 33 mm. long. The initial part of the phragmocone is missing. The dorso-ventral diameter increases from 26 mm. to 51 mm. at the second-last camera; it then remains constant until a distance of about 9 mm. from the base of the living chamber whence the diameter decreases towards the aperture. The lateral diameter increases from 26 mm. to 56 mm. at a distance of about 9 mm. from the base of the living chamber; at the second last camera the diameter is 50 mm. It will be seen, therefore, that in the dorso-ventral section the greatest gibbosity is reached in the upper part of the phragmocone whereas the greatest diameter in the lateral section is reached distinctly above the base of the living chamber. Exact shape and dimensions of the aperture cannot be determined, but its maximum lateral diameter must have been approximately 43 mm. The longitudinal outline of the conch is evenly convex dorsally; it is slightly concave along the greater part of the ventral side of the phragmocone and straight along the adoral part of the phragmocone and the adapical part of the living chamber. The dorsal side of the conch is slightly flattened, ventral and lateral sides evenly convex. The septa are only slightly concave. The sutures rise laterally, owing to the curvature of the conch, and are almost straight across the dorsum. The distance between the sutures along the dorsal side increases from about 3 mm. to 5.3 mm., but the second-last camera is only 4.1 mm., the last camera only 3.0 mm. long. The corresponding distances along the ventral side are approximately three-fifths of the distances along the dorsal side.

At the base of the living chamber there is an impressed zone in the mould immediately above the last septum. In some places remnants of the shell are still preserved in this depression which is due to an internal thickening of the shell in this place. Similar features have been noted in nautiloids, particularly in gomphoceroid conchs, by earlier observers (J. Hall, J. Barrande and others) and were lately described in detail by Flower (1938), who considers the thickening of the basal zone of the wall of the living chamber as a gerontic feature.

The siphuncle is close to the ventral wall, but no details can be seen.

(2) No. 19486, Department of Geology, University of Western Australia, from strata 12 feet above the preceding specimen in the same locality. (Pl. I., fig. 2; Pl. II., fig. 5.)

This is a larger specimen, 118 mm. long, with the shell still preserved, consisting of portion of a phragmocone with 18 camerae and an almost complete living chamber which is 49 mm. long. The dorso-ventral diameter

increases from 22.5 mm. to 63 mm. at the second-last camera. It still increases very slightly along the adapical part of the living chamber, but this is probably due to the fact that most of the shell is worn away along the upper part of the phragmocone whereas the shell of the living chamber is well preserved. There is probably no true increase in thickness of the conch above the second-last septum. The lateral diameter increases from 22 mm. to 68 mm. at the base of the living chamber and to 71 mm. at a distance of 10 mm. above the base of the living chamber. The longitudinal outline of the conch along the dorsal side is evenly convex, the ventral outline concave in the adapical part of the phragmocone and straight in the adoral part of the phragmocone and in the adapical part of the living chamber. The lateral outline is very slightly concave in the adapical part of the phragmocone, but straight along the greater part of the phragmocone and the adapical part of the living chamber. The cross-section is evenly rounded ventrally and laterally, somewhat flattened dorsally. The sutures rise along the lateral sides and are straight across the dorsum. The distance between the sutures when measured along the ventral side increases from 1.4 mm. to 5.8 mm. in the second-last camera; the last camera is only 3.4 mm. long. Measured along the dorsal side the distance of the sutures is about 1.4 times longer.

The siphuncle is quite close to the ventral wall of the conch. Its diameter is 1.5 mm. at the adapical end of the specimen, but increases rapidly to 4 mm. in the tenth camera.

The shell of the conch is apparently smooth and is rather heavy. Around the base of the living chamber, there is an internal thickening of the wall, forming a distinct ring which is 4.2 mm. wide; the inner side of the ring is vertically ribbed. The shell is here 4.0 mm. thick, whereas the normal thickness of the wall of the living chamber is slightly less than 3 mm.

The aperture is only partly preserved but can be reconstructed with a fair degree of certainty (Fig. 1). It is strongly contracted laterally to a minimum width of probably not more than 32 mm., whereas the dorso-ventral diameter of the aperture must be at least 58 mm. The shape is phragmoceroid with a straight dorsal outline, slight expansion between the dorsum and the centre to a width of at least 40 mm., a strong contraction between the centre and the venter and a strong, but probably rather wide hyponomic sinus.

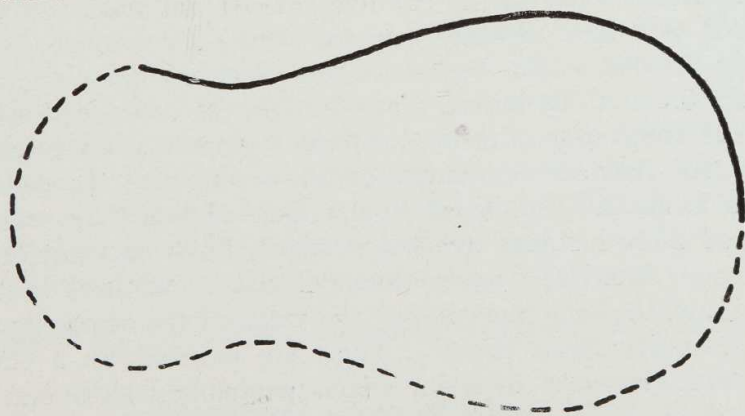


Fig. 1.—Outline of the aperture of *Wadeoceras australe* Teichert. Same specimen (No. 19486) as Pl. I., fig. 2, and Pl. II., fig. 5.

The differences between this specimen and the one described before are regarded as indicating sex distinction rather than specific separation.

(3) A fragment of a specimen of the smaller type was found 63 feet above the preceding specimen. The cross-section of its siphuncle (pl. II. fig. 6) is slightly oval with a more narrowly rounded ventral side and the presence of simple, short and not very numerous radiating lamellae is clearly indicated.

Genus **DANAOCERAS** Foerste.

Genotype—*Cyrtoceras danai* Barrande.

Danaoceras subtrigonum (McCoy).

Plate III., Figs. 7-9, Plate IV., Fig. 11.

1876 *Phragmoceras subtrigonum*, F. McCoy, Prod. Pal. Vict., Dec. IV., pl. 35, Figs. 6, 6a.

Description of holotype (No. 1290, National Museum, Melbourne): The specimen is an internal mould of portion of a phragmocone and a large part of the living chamber. The dorso-ventral diameter increases from 43 mm. at the adapical end to 60 mm. at the base of the living chamber and to 67 mm. at a distance of 20 mm. from the base of the living chamber; the corresponding figures for the lateral diameter are 40, 56 and 61 mm. Thus, the phragmocone expands at a quicker rate than the living chamber. As far as the latter is preserved there is no sign of contraction and it seems unlikely that the specimen possessed a contracted aperture. The ventral outline of the specimen is slightly, but evenly concave, its dorsal outline convex. The lateral outlines of the phragmocone are slightly convex, those of the living chamber almost straight with diverging sides. The cross-section is oval with a broadly rounded dorsal and narrowly rounded ventral side. The surface of the mould is ornamented by weak longitudinal ridges on the ventral and lateral sides; the absence of this ornamentation on the dorsal side may be due to weathering. The ridges are about 1.5 mm. apart at the base of the specimen, their distance increases adorally in accordance with the expansion of the conch. The septa are moderately convex, the sutures almost straight, except for a slight ventral saddle. Measured along the dorsal side the distance between successive sutures is 6.8, 5.9, 6.7, 4.8, 3.3, 3.7, 3.5, and 5.5 mm. It seems, therefore, that the specimen is not yet fully mature. Ventrally, the distance between the septa is approximately two-thirds the distance measured along the dorsal side.

The siphuncle is close to the concave side of the conch; at the bases of the specimen it is 2 mm. distant from the wall of the conch. In a section approximately parallel to the septum in this place the dorso-ventral diameter of a segment is 8.7 mm., its lateral diameter 5.7; the cross-section is elliptical. Attached to the inner side of the wall of the segments are a great number of lamellae, directed towards the centre of the siphuncle. Lamellae of about 1 mm. length alternate with lamellae 0.5 mm. or less long. In transverse section most of these lamellae are not straight, but somewhat irregular and bent. The longer lamellae usually divide into two or three branches. The lamellae consist of the same material as the walls of the segments and emerge without discontinuity from them. They are covered by a thin layer of apparently stereoplasmatic deposits which probably correspond to the deposits observed by Dechaseaux (1937) on the endosiphuncular lamellae of *Jovellania*.

Additional material: In another specimen from the type locality a longitudinal section through an earlier part of the phragmocone is exposed (fig. 2). The dorso-ventral diameter of this species increases

from about 13 mm. to 32 mm. The septa are only preserved in the adapical part of the specimen where they are 1.5 mm. apart. The ventral outline is slightly concave, the dorsal outline slightly convex. The siphuncle is close to the ventral wall. The segments are only slightly expanded between the septa. The first of the segments which can be measured is 1.5 mm. long and 1.4 mm. wide; the last segment preserved is 3.0 mm. long and 3.8 mm. wide. Vertical lamellae are visible in the interior of the siphuncle. This specimen represents a portion of the phragmocone almost in the immediate adapical continuation of the phragmocone of the holotype.

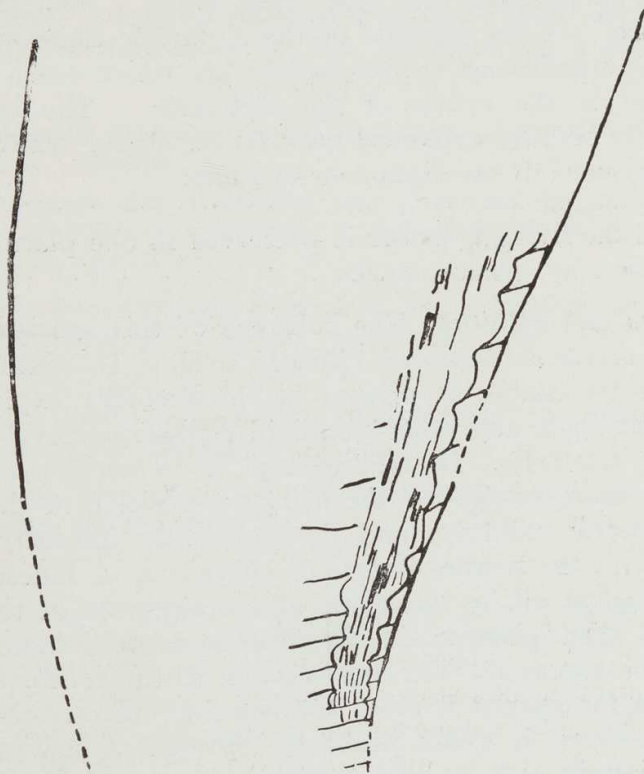


Fig. 2.—Cross-section of adapical part of phragmocone of *Danaoceras subtrigonum* McCoy. Buchan, East Gippsland, Victoria. National Museum, Melbourne. 2.3 X.

Comparisons and affinities: This species agrees in many respects with the holotype of *Danaoceras*, *D. danai* Barrande, from the Middle Silurian of Bohemia, an endogastric cyrtoceracone with unconstricted aperture (Foerste 1926, p. 246). It differs from that species in the presence of weak internal longitudinal ribs and probably also in the relative width of the siphuncle which is described as cylindroid “not only along the lower part of the phragmocone, but also farther up” (Foerste 1926, p. 347). However, until a detailed study of the structure of the siphuncle of the genotype has been made, the two species can be regarded as congeneric.

Occurrence: In the Middle Devonian limestone of Buchan, Gippsland, Victoria.

***Danaoceras* (?) *bindiense* sp. nov.**

Plate I., Fig. 1, Plate IV., Figs. 10, 12.

Description of holotype (No. 1293, National Museum, Melbourne): The specimen is an internal mould of portion of a phragmocone with ten camerae and the basal part of the living chamber. The dorso-ventral diameter of the

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phragmocone increases from 28 mm. to approximately 43 mm.; the actual figures are probably 2 or 3 mm. larger, since the ventral side of the mould is somewhat weathered and the siphuncle exposed. The lateral diameter of the phragmocone increases from 27 mm. to approximately 44 mm., and the cross-section, therefore, must have been very slightly compressed in the original conch. The conch seems to be straight, but may have been slightly concave ventrally, and the living chamber which in one place is preserved for a length of 15 mm. expands at almost the same rate as the phragmocone. The sutures are straight and the height of the successive camerae is 3.5, 3.5, 3.2, 3.4, 3.0, 3.3, 2.7, 2.5, 3.7, 3.0 mm. The septa are very slightly convex. The siphuncle was probably not more than about 1 mm. from the ventral wall of the conch. In the interior of the siphuncle there are a number of vertical lamellae, numbering approximately 25, which reach from the periphery very close to the centre of the siphuncle. The segments of the siphuncle are only slightly expanded between the septa. The lateral diameter of the second segment of the siphuncle is 5 mm.

The shell of the living chamber is preserved in one place where it shows transverse striation by growth marks.

Comparisons and affinities: The holotype of this species was originally listed as *Phragmoceras subtrigonum* (Benson 1922, p. 114; Hills 1935, p. 113). Its generic affinities cannot at present be satisfactorily explained, but it is certainly different from any other nautiloid cephalopod so far known from the Devonian of Australia. Its relationships to *Danaoceras subtrigonum* are not particularly close, except for the marginal position of the siphuncle, its probably endogastric affinities, and its apparently unconstricted aperture. The difference is in the smaller degree of curvature, if, indeed the Victorian specimen is curved at all, in the shape of the segments of the siphuncle, in the structure of the siphuncle, in the absence of longitudinal ribs on the mould, and in the almost circular cross-section of the conch. If future finds should show that the species is erect and has a circular cross-section and an unconstricted aperture, it would probably represent a new genus of actino-siphonate cephalopods.

Occurrence: Middle Devonian of Bindi, East Gippsland, Victoria.

PLATE I.

All figures natural size.

Fig. 1. *Danaoceras ? bindiense* sp. nov. Holotype. Adapical view. Middle Devonian, Bindi, East Gippsland, Victoria. No. 1293, National Museum, Melbourne.

Fig. 2. *Wadeoceras australe* Teichert. Supposed female, lateral view. Upper Devonian, near Mount Pierre, West Kimberley District, Western Australia. No. 19486, Department of Geology, University of Western Australia.

Fig. 3. *Wadeoceras australe* Teichert. Supposed male, lateral view. Same locality as Fig. 2. No. 19485, Department of Geology, University of Western Australia.

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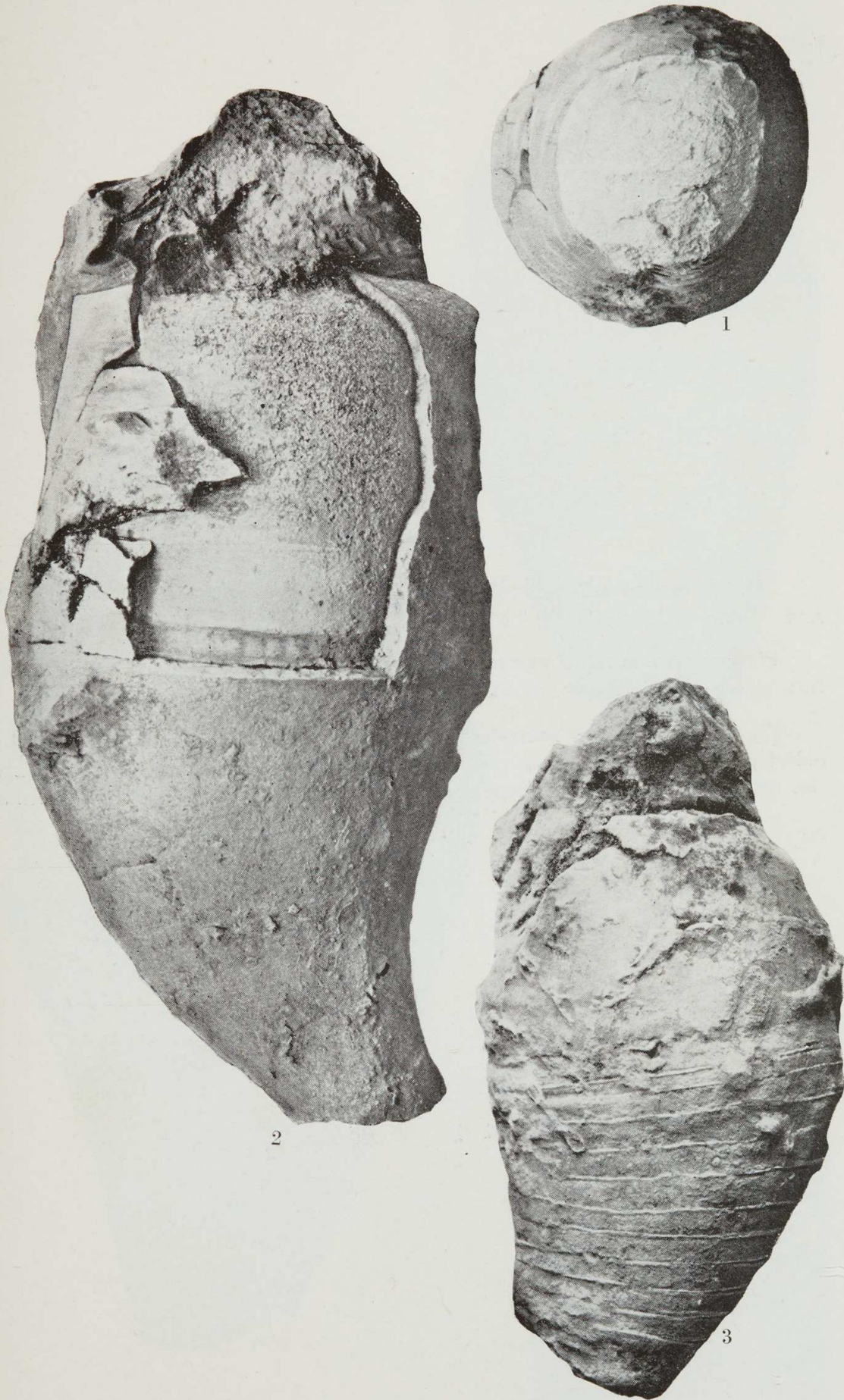


PLATE I.

PLATE II.

Fig. 4. **Wadeoceras australe** Teichert. Supposed male, ventral view. Nat. size. Same specimen as Pl. I., Fig. 3.

Fig. 5. **Wadeoceras australe** Teichert. Supposed female, ventral view. Nat. size. Same specimen as Pl. I., Fig. 2.

Fig. 6. **Wadeoceras australe** Teichert. Cross-section of siphuncle showing radiating lamellae, 9 ×, made from another male specimen, found 63 feet above No. 19486. No. 19497, Department of Geology, University of Western Australia.

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PLATE III.

All figures natural size.

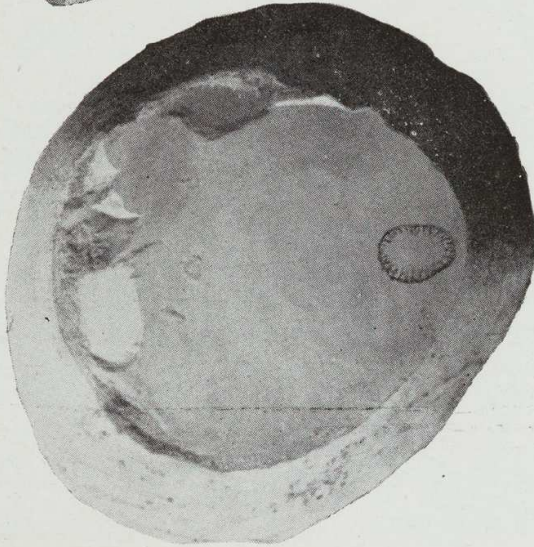
Figs. 7-9. *Danaoceras subtrigonum* McCoy. Holotype. Ventral, adapical, and lateral views, nat. size. Middle Devonian, Buchan, East Gippsland, Victoria. No. 1290, National Museum, Melbourne.

(N.B.—The siphuncle did not appear on the original photo of Fig. 8 and is shown diagrammatically; its structure is identical with that shown on Pl. IV., Fig. 11.)

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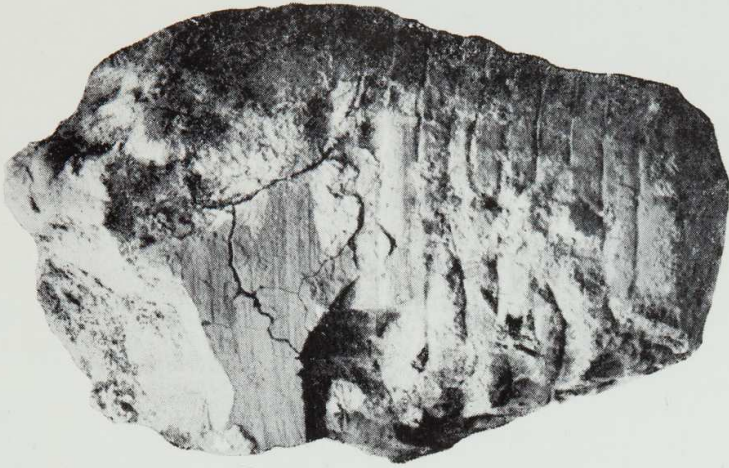
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PLATE IV.

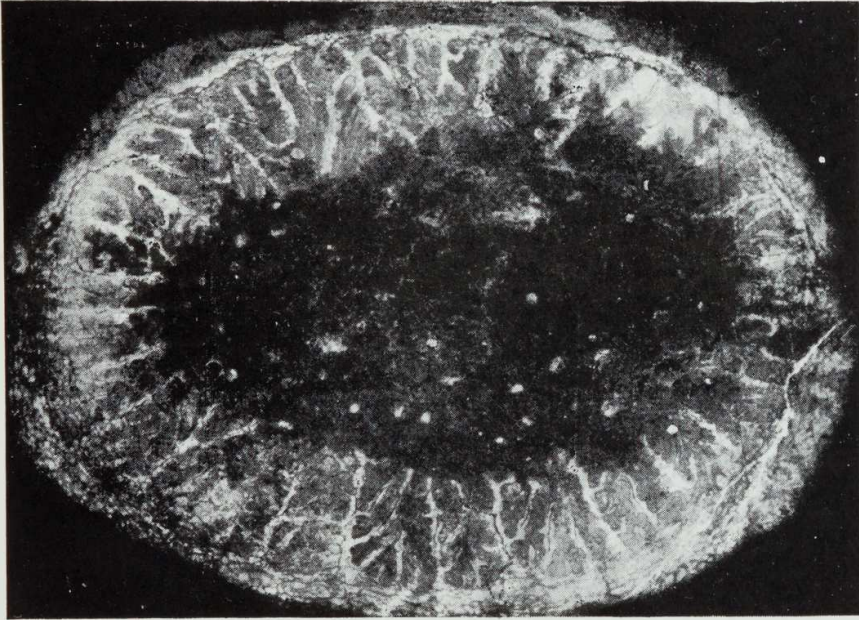
Figs. 10, 12. *Danaoceras ? bindiense* sp. nov. Holotype. Ventral and lateral views, nat. size. Same specimen as Pl. I., Fig. 1.

Fig. 11. *Danaoceras subtrigonum* McCoy. Cross-section of siphuncle of another specimen, 7 ×. Same locality as holotype. No. 1291, National Museum, Melbourne.

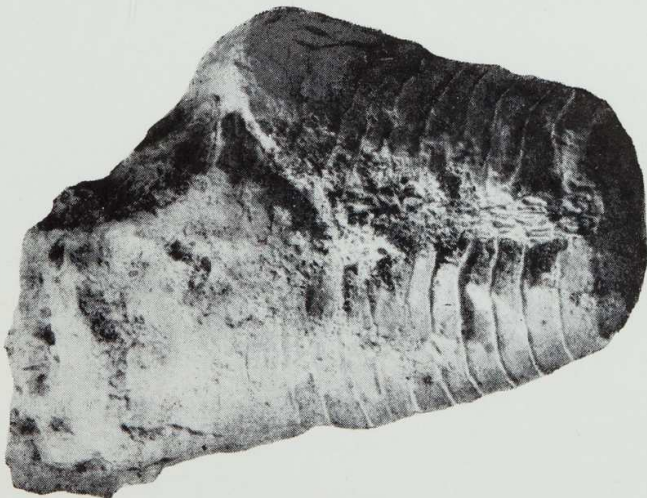
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